

Assessing multi-taxa sensitivity to the human footprint, habitat fragmentation and loss by exploring alternative scenarios of dispersal ability and population size: a simulation approach

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Abstract Quantifying the effects of landscape change on population connectivity is compounded by uncertainties about population size and distribution and a limited understanding of dispersal ability for most species. In addition, the effects of anthropogenic landscape change and sensitivity to regional climatic conditions interact to strongly affect habitat fragmentation and loss. To further develop conservation theory and to understand the interplay between all of these factors, we simulated habitat fragmentation and loss across the Western United States for several hypothetical species associated with four biome types, and a range of habitat requirements and dispersal abilities. We found dispersal ability and population size of the focal species to be equally sensitive to habitat extent, while dispersal ability is more sensitive to habitat fragmentation. There were also strong critical threshold effects where habitat connectivity decreased disproportionately to decreases in life-history traits making these species near these thresholds more sensitive to changes in habitat loss and fragmentation. Overall, grassland and forest associated species are also most at risk from habitat loss and fragmentation driven by human related land-use. These two largest biome types were most sensitive at large contiguous patch sizes which is often considered most important for metapopulation viability and biodiversity conservation. Hypothetical simulation studies such as this can be of great value to scientists in further conceptualizing and developing conservation theory, and evaluating spatially-

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explicit scenarios of habitat connectivity. Our results are available for download in a web-based interactive mapping prototype useful for accessing the results of this study.

Keywords Connectivity modeling · Least-cost paths · Resistant kernels · UNICOR

Introduction

Habitat fragmentation and loss threaten biodiversity, decrease dispersal rates and increase mortality of wildlife populations (Fahrig et al. 1995; Frankham et al. 2002; Crooks and Sanjayan 2006; Allendorf et al. 2013). Despite increasing interest and motivation for increasing population connectivity in response to increased threat of habitat fragmentation and loss (Franklin 1993; Crooks and Sanjayan 2006), empirical dispersal data are lacking for most species across large spatial scales (Bowne and Bowers 2004). Yet metapopulation viability is best addressed on large spatial scales for multiple species because of the ecological and evolutionary adjustments occurring at these scales (e.g., climate change; Soulé et al. 2006). There is a need for broad-scale, flexible, biome associated approaches for exploring the underlying theory of population connectivity without requiring species specific empirical data (Roberge and Angelstam 2004; Cushman and Landguth 2012). Here, we demonstrate the use of a biome-associated, resistance kernel model for assessing multi-taxa habitat connectivity for the entire Western United States.

Much of the difficulty in predicting the effects of landscape change on population connectivity is due to uncertainty about species population sizes and distributions, how different landscape features affect movement, and limited understanding of species dispersal abilities (Cushman et al. 2013). Past studies in this realm do not distinguish between the interaction of population size, dispersal ability and landscape resistance on the extent versus the fragmentation of connected habitat (Compton et al. 2007; Cushman et al. 2010). This distinction is important given that the interpretation and management response to a given change will differ substantially depending on whether it is loss or fragmentation driven (McGarigal and Cushman 2002; Fahrig 2003). Considering habitat fragmentation in terms of the change in contiguous habitat may also be important because of greatly varying life-history traits (e.g., limited gap crossing ability), and similarly, contiguous habitat has direct effect on area sensitive species (Freemark and Merriam 1986; Robbins et al. 1989). Contiguous habitat may also impact species diversity as smaller patch sizes can contain fewer species than larger patches, with small patches containing only a subset of species found in larger patches (Vallan 2000; Debinski and Holt 2000; Fahrig 2003). Finally, large, interconnected patch networks are key “stepping stones” for long-distance movements and for preserving broad-scale population connectivity (Soulé et al. 2006).

Quantitative approaches for understanding population connectivity in recent years have focused on landscape as a weighted resistance surface that represents the relative impediment different landscapes impose on specific species (Spear et al. 2010; Zeller et al. 2012). Consequent connectivity analysis is then often focused on calculating a path or corridor (e.g. least cost) based on the weighted resistance surface. However, the least cost or path related approaches are often limited as it is unclear how effective least-cost paths or corridors are in protecting functional connectivity across full, complex landscapes (Sawyer et al. 2011). An alternative approach is to consider all possible routes by creating a dispersal resistance kernel (Compton et al. 2007; Cushman et al. 2010). Resistant kernel

connectivity modeling is a more robust approach because it is spatially synoptic and predicts expected probabilities of dispersal (or rates of migration) for every pixel in the study area extent. The other major advantage of resistance kernel modeling is it can be used to study multi-taxa connectivity for vast geographical regions (Cushman and Landguth 2012).

Here we illustrate the use of resistant kernel connectivity modeling to help better understand general species sensitivity to habitat loss and fragmentation given varied life-history traits (dispersal ability and population size). Our major goal was to map the extent and fragmentation of connected populations of several terrestrial species occupying four major biome types in the Western United States. Additionally, we explored three major scenarios of the human impact on habitat fragmentation and loss in: (1) a “pristine” or no human impact, (2) a low human influence scenario, and, (3) a high human influence scenario. In total, we tested 48 different simulations of habitat connectivity across the largest extent yet attempted in a resistant kernel modeling study. We offer results of our simulations by answering three major research questions:

- (1) Does lower dispersal ability more than smaller population size increase species sensitivity to habitat loss and fragmentation?
- (2) What biome type(s) is/are most impacted by the human footprint (roads and land-use)?
- (3) Does the human footprint scenarios have a larger impact on habitat fragmentation or loss?

Methods

Study system

The study system covered the conterminous Western United States from 100° longitude westward (Fig. 1). This region includes most of the federally protected land and forested areas in the conterminous United States. Also, many important wildlife preserving National parks are found in this region including the Yellowstone, Glacier, Yosemite, Redwood, and Mount Rainer National parks.

Vegetation class data

The original vegetation data were from the Mapped Atmosphere-Plant-Soil System (MAPSS; <http://www.fs.fed.us/pnw/mdr/mapss/>) vegetation model (Neilson 1993, 1995; Neilson and Marks 1994). MAPSS is a vegetation distribution model developed to simulate potential biosphere impacts and biosphere–atmosphere feedbacks from climate change. Output from MAPSS has been used extensively in the Intergovernmental Panel on Climate Change’s (IPCC) regional and global assessments of climate change. From the MAPSS model, vegetation was reclassified from the original 10 km resolution climate data model including 62 vegetation classes (Table 1) into four broadly inclusive biomes; Grassland/Shrubland (GS), Mixed Conifer (MC), Desert (DE) and Sub-alpine (SA). The reclassified data were then interpolated to 1 km resolution using bilinear interpolation.

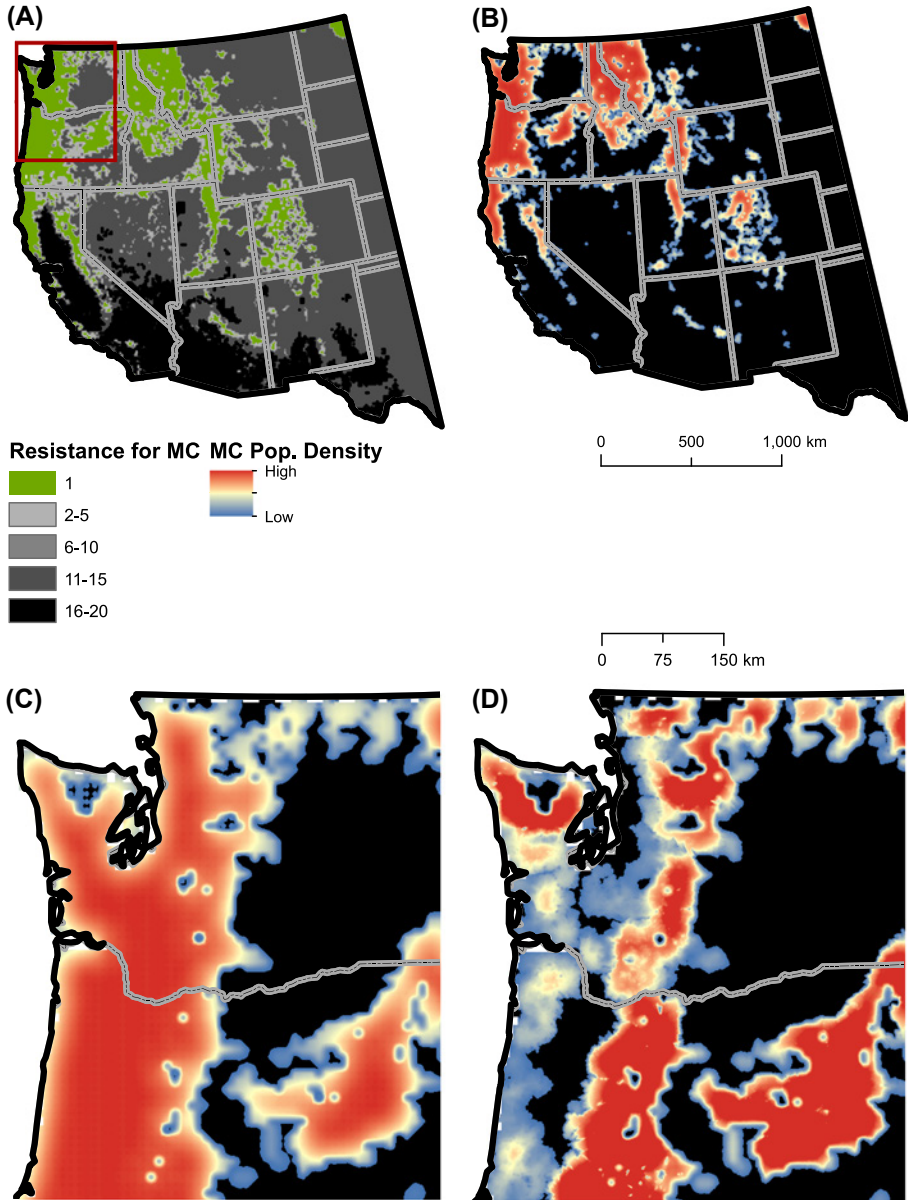


Fig. 1 A map of the Western United States highlighting the mixed conifer (MC) biome. **a** Base resistance map for the Western United States for MC; all resistances in green are equal to 1. **b** Resistant kernel map for the entire study area using the null model showing the variation in predicted population density in blue-red. **c** An extent of the West Coast centered over Washington State, using the null or “pristine” resistance kernel model. **d** The same extent as c but showing the difference in population density of the high human footprint model. (Color figure online)

Table 1 Cover and biome types with assigned resistance values used in the kernel resistance simulation

| Resistances by cover or biome type | Scenario | | | |
|---|----------|-----|----|----|
| | LHF | HHF | | |
| Land cover | | | | |
| <i>Natural</i> Perennial ice/snow; barren land; deciduous forest; evergreen forest; mixed forest; scrub/shrub; herbaceous; emergent herbaceous wetlands; woody wetlands | 1 | 1 | | |
| <i>Agricultural</i> Hay/pasture; cultivated crops; open water | 5 | 15 | | |
| <i>Residential</i> Developed; open space; developed; low intensity | 5 | 15 | | |
| <i>Urban</i> Developed; medium intensity; developed; high intensity | 10 | 20 | | |
| Road cover | | | | |
| <i>Primary highway with limited access</i> Interstate highways and some toll highways with interchanges | 50 | 80 | | |
| <i>Primary road without limited access</i> US highways, some state highways and county highways that connect cities and larger towns | 30 | 50 | | |
| <i>Secondary and connecting road</i> State highways, county highways that connect smaller towns, subdivisions, and neighborhoods | 10 | 20 | | |
| <i>Local, neighborhood, and rural road</i> Local traffic, single lane | 2 | 5 | | |
| <i>Vehicular trail</i> Roads usable only by four-wheel drive vehicles, one-lane dirt trails in rural areas | 2 | 5 | | |
| <i>Road with special characteristics</i> Portions of a road, intersections of a road, or the ends of a road that are parts of the vehicular highway system and have separately identifiable characteristics | 2 | 5 | | |
| <i>Road as other thoroughfare</i> Foot and hiking trails located on park and forest land | 2 | 5 | | |
| Biome resistances | GS | MC | DE | SA |
| Grass/Shrub | | | | |
| Shrub Savanna (Deciduous Broadleaf, Mixed Warm, Mixed Cool, Evergreen Micro) | 1 | 15 | 10 | 20 |
| Shrubland Temperate (Conifer, Xeromorphic Conifer); Grass (Short, Mid, Tall); Grass Dry (Short, Mixed Short); Grass Prairie (Short, Tall); Grass Northern (Short, Tall, Mixed Mid, Mixed Tall); Grass Southern (Mixed Mid); Open Shrubland (No Grass) | 1 | 15 | 5 | 20 |
| Shrub Savanna Tropical | 1 | 20 | 10 | 25 |
| Chaparral | 1 | 10 | 5 | 10 |

Table 1 continued

| Biome resistances | GS | MC | DE | SA |
|--|----|----|----|----|
| Mixed conifer | | | | |
| Forest Evergreen Needle (Tiaga, Maritime, Continental) | 15 | 1 | 20 | 5 |
| Tree Savanna (Mixed Cool, Mixed Warm, Evergreen Needle Maritime, Evergreen Needle Continental) | 10 | 1 | 15 | 10 |
| Forest Mixed Warm | 15 | 1 | 20 | 10 |
| Desert | | | | |
| Grassland Semi Desert; Desert Boreal | 5 | 20 | 1 | 25 |
| Desert (Subtropical, Tropical, Extreme) | 10 | 20 | 1 | 25 |
| Subalpine | | | | |
| Taiga/Tundra | 20 | 5 | 25 | 1 |
| Tundra | 25 | 15 | 30 | 1 |
| Other | | | | |
| Tree Savanna PJ Continental; Tree Xeric Continental Savanna PJ Maritime; Tree Savanna PJ | 5 | 10 | 5 | 10 |
| Shrub Savanna SubTropical Mixed | 15 | 20 | 5 | 10 |
| Shrubland SubTropical (Xeromorphic, Mediterranean) | 20 | 25 | 5 | 10 |
| Desert temperate | 20 | 25 | 5 | 5 |
| Tree Savanna (Deciduous Broadleaf, Mixed Warm) | 5 | 10 | 10 | 15 |
| Forest (Deciduous Broadleaf, Mixed Warm, Mixed Cool) | 5 | 10 | 15 | 20 |
| Forest Hardwood Cool | 5 | 10 | 15 | 20 |
| Forest (Evergreen Broadleaf Tropical, Seasonal Tropical, Savanna Dry Tropical) | 10 | 15 | 20 | 20 |
| Ice | 20 | 5 | 25 | 30 |

Numbers under scenario refers to the resistance values assigned to land cover or road cover class for the *LHF* low human footprint or *HHF* high human footprint scenario. Biome abbreviations are *GS* grassland/shrub, *MC* mixed conifer, *DE* desert, *SA* subalpine. The resistance values differ for each biome type and are organized by land types assumed to be native to each biome type, and a category of other land types which are not native to any biome

Road and land cover data

Road and land coverages for the Western United States were taken from the Census 2000 TIGER line files (<http://www.census.gov/geo/www/tiger/tiger2k/tgr2000.html>) and the 2001 National Land Cover Database at <http://www.mrlc.gov/nlcd.php> (UA Census 2000; Homer et al. 2007). The purpose of the road and land cover layers was not to assess habitat suitability, (which was already addressed by the biome layer), but as a measure of the human footprint on resistance to dispersal. Different land-use types (e.g., agriculture and urban centers) carry respectively higher resistances (Table 1). Water was also considered to be higher resistance, since the focus was on terrestrial species.

Road cover was taken from a vector map of all major and minor roadways from the 2000 Census. The data were converted to a 30 m resolution raster map. Road features were reclassified (Table 1) and smoothed to 1 km resolution using a 50 × 50 moving window in the focal statistics toolkit in ArcGIS (Esri 2011). Land cover was bilinearly interpolated from 30 m to 1 km resolution before being combined with the roads and biomes layers to have all layers at the same grid resolution. All dataset creation and interpolation was done in the ArcGIS 10 (ESRI 2011) and/or using the library ‘raster’ (Hijmans and van Etten 2013) in the statistical software package R (R Core Team 2013).

Resistant kernel connectivity modeling

For each scenario of biome association and human footprint impact, predictions for habitat connectivity were based on a least-cost resistant kernel approach implemented in UNICOR v2.0 (Compton et al. 2007; Cushman et al. 2010; Landguth et al. 2012). Unlike most corridor prediction efforts, the resistant kernel approach is spatially synoptic and provides prediction and mapping of expected dispersal rates for every pixel in the study area extent, rather than only for a few selected “linkage zones” (Compton et al. 2007). Also, in resistant kernel modeling scale dependency of dispersal ability can be directly included to assess how species of different vagilities may be affected by landscape fragmentation. Resistant kernel modeling is also computationally efficient, enabling simulation and mapping across the entire Western United States for multiple species (Cushman et al. 2010).

All resistance scenarios below provide values for all locations in the study area, in the form of the cost of crossing that pixel. Cost-distances then refer to the cumulative cost of traveling from a source point to any other location. These cost distances are used as weights in the dispersal function, such that the expected density of dispersing individuals in a pixel is down-weighted by the cumulative cost from the source, following the least-cost route (Compton et al. 2007). The initial expected density was set to one for each source cell. The predicted density in each surrounding cell is predicted density relative to the maximum at a source cell. The model calculates the expected relative density of each species in each pixel around the source, given the dispersal ability of the species, the nature of the dispersal function, and the resistance of the landscape (Compton et al. 2007; Cushman et al. 2010).

The UNICOR v2.0 (Landguth et al. 2012) program used a scaled resistant kernel value so kernel volume was constant (which equates to a constant population size at all occupied source locations). Thus, volume was kept constant across different dispersal abilities and assured that more mobile species were not misconstrued to have larger population sizes. Our approach was somewhat similar to Compton et al. (2007) where a normal probability

density function was used as a basis of the dispersal model. Here, we assumed a linearly scaled dispersal function dependent on cost distance.

Modeling scenarios

Three modeling scenarios were assessed; the null or “pristine” scenario, a low human footprint (LHF), and a high human footprint (HHF). The “pristine” scenario considered only the resistances of the biome resistance maps for each specific biome (GS, MC, DE and SA) without the influence of roads or land cover (Table 1; Fig. 1). Each biome was assumed to be a natural habitat for some species and each pixel in that biome to have an associated value of one compared to other, less desirable habitats for those same species (i.e., resistance values of one refer to the easiest traversable areas on each landscape). When a species entered a non-native habitat it was assigned additional resistance penalty per pixel and based on the native habitat of the species (Table 1). Extreme differences in biomes were assumed to represent large resistance differences. For example, DE species have a high resistance in SA and MC biomes and vice versa. Values were based on expert opinion; which was appropriate in this case given the lack of species-specific resistance relationship data across the extent of our study and our goal to represent a broad range of plausible species responses (Table 1; Sawyer et al. 2011).

The LHF and HHF scenarios included roads and land cover as separate resistance maps, in addition to the biome resistance map (Table 1). Points were seeded at every 10 km and only where the resistance map had a value of one (i.e., indicative of where the habitat-associated species occurred). For the LHF and HHF, this was consistent with an animal choosing its preferred biome type and natural habitat without roads. For each of the biomes in the null model starting locations (seeded points) consisted of 22,667 for GS; 6,895 for MC; 4,085 for DE; and 627 for SA. Four dispersal distances (12.5, 25, 37.5 and 50 km) were considered for each of the scenarios and biomes for a total of 48 different resistance scenarios.

FRAGSTATS analysis of modeling scenarios

Different population sizes were produced of 625, 2500, and 10000 individuals per 100 square kilometers. A binary map of presence/absence in the study area was used for further analysis in the FRAGSTATS program (McGarigal et al. 2013). To do this cells were considered occupied only if cell values were greater than 0.00001 (corresponding to a minimum of one individual per 10 square km).

The FRAGSTATS program was used to calculate four class-level metrics to compare the scenarios in their impact on the extent and fragmentation of connected habitat: (1) the extent of connected habitat as a proportion of the total study area (PLAND), (2) number of patches of connected habitat (NP), (3) correlation length of connected habitat (CL, denoted as GYRATE_AM in FRAGSTATS), (4) the size of the largest patch as a proportion of the total study area (LPI). The PLAND metric is a quick and useful measure for the comparative measure of the amount of loss of habitat extent between different scenarios. The NP quantifies fragmentation of connected habitat in each scenario. The CL metric is the area-weighted mean radius of gyration, where the mean radius of gyration is the mean distance between each cell in a patch and the patch centroid. The CL gives the expected distance of travel while staying in that particular patch type, from a random starting point and moving in a random direction. The LPI metric provides a direct measure of the extent of the largest connected patch of habitat for each scenario.

Results

Percentage of the total land area (PLAND)

There was a non-linear trend of the decreasing extent of connected habitat (PLAND) as population size and dispersal ability decreased that accelerated as both life history traits decreased (Table 2). PLAND tended to decrease more slowly with decreases in the other life history trait, however, when at low population size or dispersal ability. In other words, the two factors interact. This reverse in trend suggested the combination of life history traits had a compounding effect, but only up to a certain threshold where PLAND was much less responsive to changes in life history traits. For the SA biome, the greatest change in PLAND occurred at the minimum population size and highest dispersal ability where the value decreased 62 % from its maximum (from 3.4 to 1.3 %). For the GS, MC and DE scenarios, the decrease in the maximum value of PLAND from high to low values of dispersal ability and population size was 18, 28 and 22 % respectively.

Number of patches (NP)

Across all biome types and population sizes, dispersal ability had a much greater sensitivity to the number isolated patches of habitat internally connected by dispersal than did population size. The increase in NP was non-linear along dispersal gradients and tended to accelerate at low (12.5–25 km) dispersal ability [e.g., at low population sizes NP increased with decreased dispersal ability in ratios of 80:1 (GS), 11:1 (MC), 9:1 (DE) and 6:1 (SA), Table 2]. Along constant levels of dispersal ability, NP tended to peak at medium population sizes (2,500) for mid-range dispersal abilities (25–37.5 km) and then greatly decreased thereafter. The resulting decrease from medium to low population sizes in NP was often quite large with as much as a 94 % loss (Table 2) and in many cases was >50 %. The only exception to this sharp decline in NP was at the lowest dispersal ability, where NP tended to remain unchanged (GS, DE, and SA) or slightly increased (MC).

Correlation length (CL)

Dispersal ability had more effect on CL than did population size (Table 2) as the relative changes between the extremes in life history traits (high dispersal ability and population size to either low population size or low dispersal, while keeping the other variable constant) showed a larger difference along the dispersal ability gradient (Table 2). For all four biome types there were distinct threshold effects where correlation length of connected habitat dropped dramatically in response to changes in population size or dispersal ability, with the tendency to slow or stop for further decreases (with the exception of the SA biome that had several large decreases). Values dropped for CL at these various thresholds in a range between 7 % (DE) and 31 % (MC).

Largest patch index (LPI)

The LPI metric decreased non-linearly with decreased dispersal ability and population size for all biome types. The LPI and CL metrics appeared to correlate strongly for the GS and MC biome types (Table 2). For both GS and MC, strong threshold patterns were present at identical dispersal ability and population sizes for both LPI and CL. This was to be

Table 2 Effects of dispersal ability and population size on four graph metrics: (1) percentage of total land area (PLAND), (2) number of patches (NP), (3) CL (GYR-ATE_AM), (4) largest patch index (LPI)

| | Disp. dist. (k) | Low pop. (625) | | | Med. pop. (2,500) | | | High pop. (10,000) | | |
|---------------------------------------|-----------------|----------------|------|------|-------------------|------|------|--------------------|------|------|
| | | Null | LHF | HHF | Null | LHF | HHF | Null | LHF | HHF |
| | | | | | | | | | | |
| Percentage of total landscape (PLAND) | | | | | | | | | | |
| GS | 12.5 | 53.2 | 39.0 | 33.6 | 54.7 | 41.6 | 36.3 | 55.1 | 42.2 | 99.5 |
| | 25 | 54.1 | 40.4 | 34.9 | 58.4 | 47.7 | 42.2 | 60.1 | 50.1 | 44.5 |
| MC | 37.5 | 54.9 | 40.8 | 35.0 | 59.9 | 49.9 | 44.2 | 62.8 | 54.2 | 48.3 |
| | 50 | 55.3 | 41.1 | 35.0 | 60.4 | 51.1 | 45.2 | 64.5 | 56.6 | 50.5 |
| DE | 12.5 | 17.3 | 14.6 | 12.2 | 18.2 | 15.7 | 13.5 | 18.5 | 16.0 | 13.9 |
| | 25 | 18.1 | 15.4 | 14.6 | 20.5 | 18.5 | 16.7 | 21.4 | 19.5 | 17.8 |
| SA | 37.5 | 18.5 | 15.6 | 17.3 | 21.6 | 19.5 | 17.8 | 22.9 | 21.2 | 19.8 |
| | 50 | 18.5 | 15.5 | 12.6 | 22.2 | 20.2 | 18.4 | 24.0 | 22.3 | 21.0 |
| Number of patches (NP) | 12.5 | 10.4 | 8.3 | 7.6 | 10.7 | 8.8 | 8.2 | 10.8 | 9.0 | 8.3 |
| | 25 | 10.6 | 8.6 | 7.9 | 11.7 | 10.0 | 9.5 | 12.1 | 10.5 | 10.0 |
| GS | 37.5 | 10.8 | 8.7 | 8.0 | 12.2 | 10.5 | 9.9 | 12.9 | 11.4 | 10.8 |
| | 50 | 10.9 | 8.6 | 7.9 | 12.4 | 10.8 | 10.1 | 13.4 | 12.0 | 11.4 |
| MC | 12.5 | 1.4 | 1.4 | 1.3 | 1.6 | 1.5 | 1.4 | 1.7 | 1.6 | 1.5 |
| | 25 | 1.4 | 1.4 | 1.2 | 2.2 | 2.1 | 2.0 | 2.5 | 2.4 | 2.3 |
| DE | 37.5 | 1.4 | 1.3 | 1.2 | 2.4 | 2.3 | 2.2 | 3.0 | 2.9 | 2.8 |
| | 50 | 1.3 | 1.2 | 1.1 | 2.4 | 2.3 | 2.2 | 3.4 | 3.3 | 3.1 |
| SA | 12.5 | 2,724 | 962 | 844 | 2,724 | 861 | 715 | 2,473 | 770 | 3 |
| | 25 | 107 | 197 | 234 | 1,682 | 290 | 325 | 1,571 | 234 | 271 |
| Number of patches (NP) | 37.5 | 68 | 99 | 112 | 1,344 | 201 | 253 | 1,178 | 134 | 178 |
| | 50 | 34 | 49 | 50 | 127 | 88 | 100 | 875 | 88 | 129 |

Table 2 continued

| | Disp. dist. (k) | Low pop. (625) | | | Med. pop. (2,500) | | | High pop. (10,000) | | |
|---|-----------------|----------------|-----|-----|-------------------|-----|-----|--------------------|-----|-----|
| | | Null | LHF | HHF | Null | LHF | HHF | Null | LHF | HHF |
| | | MC | 478 | 359 | 401 | 476 | 340 | 344 | 368 | 299 |
| | 25 | 106 | 135 | 185 | 144 | 155 | 169 | 131 | 137 | |
| | 37.5 | 66 | 96 | 165 | 131 | 128 | 124 | 102 | 103 | |
| | 50 | 41 | 58 | 63 | 63 | 69 | 80 | 72 | 74 | |
| DE | 12.5 | 140 | 158 | 173 | 140 | 146 | 120 | 131 | 144 | |
| | 25 | 41 | 64 | 61 | 99 | 102 | 74 | 87 | 91 | |
| | 37.5 | 32 | 41 | 38 | 67 | 81 | 54 | 69 | 74 | |
| | 50 | 16 | 20 | 18 | 32 | 42 | 50 | 59 | 67 | |
| SA | 12.5 | 119 | 119 | 119 | 119 | 118 | 118 | 117 | 114 | |
| | 25 | 56 | 55 | 54 | 95 | 93 | 89 | 90 | 88 | |
| | 37.5 | 38 | 36 | 33 | 89 | 88 | 69 | 68 | 71 | |
| | 50 | 21 | 20 | 20 | 45 | 46 | 57 | 56 | 55 | |
| Correlation length ($\times 10^5$ m; CL) | | | | | | | | | | |
| GS | 12.5 | 498 | 416 | 373 | 493 | 413 | 493 | 414 | 744 | |
| | 25 | 502 | 430 | 393 | 495 | 589 | 609 | 590 | 586 | |
| | 37.5 | 505 | 439 | 424 | 615 | 597 | 607 | 603 | 588 | |
| | 50 | 509 | 490 | 434 | 621 | 606 | 615 | 620 | 596 | |
| MC | 12.5 | 218 | 206 | 140 | 216 | 205 | 216 | 205 | 142 | |
| | 25 | 223 | 212 | 150 | 219 | 219 | 222 | 219 | 206 | |
| | 37.5 | 225 | 218 | 158 | 319 | 220 | 319 | 224 | 209 | |
| | 50 | 231 | 222 | 185 | 322 | 224 | 321 | 319 | 223 | |

Table 2 continued

| | Disp. dist. (k) | Low pop. (625) | | | Med. pop. (2,500) | | | High pop. (10,000) | | |
|--|-----------------|----------------|-------|-------|-------------------|-------|-------|--------------------|-------|-------|
| | | Null | LHF | HHF | Null | LHF | HHF | Null | LHF | HHF |
| | | DE | 12.5 | 1.65 | 1.36 | 1.25 | 1.64 | 1.36 | 1.32 | 1.64 |
| | 25 | 1.66 | 1.45 | 1.44 | 1.64 | 1.64 | 1.60 | 1.63 | 1.65 | 1.60 |
| | 37.5 | 1.68 | 1.67 | 1.66 | 1.65 | 1.67 | 1.67 | 1.75 | 1.65 | 1.67 |
| | 50 | 1.70 | 1.70 | 1.70 | 1.77 | 1.70 | 1.69 | 1.75 | 1.68 | 1.69 |
| SA | 12.5 | 0.227 | 0.226 | 0.215 | 0.226 | 0.226 | 0.224 | 0.226 | 0.226 | 0.224 |
| | 25 | 0.245 | 0.245 | 0.243 | 0.288 | 0.288 | 0.290 | 0.294 | 0.286 | 0.288 |
| | 37.5 | 0.266 | 0.266 | 0.262 | 0.303 | 0.296 | 0.298 | 0.357 | 0.358 | 0.344 |
| | 50 | 0.336 | 0.335 | 0.328 | 0.383 | 0.374 | 0.373 | 0.426 | 0.426 | 0.429 |
| Largest patch index (% of sum of patches; LPI) | | | | | | | | | | |
| GS | 12.5 | 39.6 | 24.7 | 19.2 | 40.1 | 26.0 | 21.0 | 40.4 | 26.5 | 100.0 |
| | 25 | 40.4 | 26.4 | 21.1 | 42.5 | 43.5 | 38.8 | 55.3 | 45.6 | 40.7 |
| | 37.5 | 41.1 | 27.2 | 22.4 | 55.7 | 45.9 | 41.1 | 57.5 | 49.9 | 44.2 |
| | 50 | 41.6 | 29.9 | 23.0 | 56.4 | 47.6 | 42.5 | 59.6 | 53.1 | 46.6 |
| MC | 12.5 | 7.78 | 6.69 | 5.42 | 8.07 | 7.10 | 5.92 | 8.20 | 7.21 | 6.07 |
| | 25 | 8.21 | 7.22 | 6.05 | 9.05 | 8.33 | 7.76 | 9.54 | 8.74 | 8.20 |
| | 37.5 | 8.51 | 7.50 | 6.26 | 15.5 | 8.82 | 8.30 | 16.2 | 9.45 | 8.89 |
| | 50 | 8.71 | 7.65 | 6.40 | 15.9 | 9.20 | 8.61 | 16.9 | 15.8 | 9.40 |
| DE | 12.5 | 5.34 | 4.46 | 3.76 | 5.43 | 4.66 | 4.27 | 5.46 | 4.71 | 4.32 |
| | 25 | 5.45 | 4.68 | 4.32 | 5.69 | 5.25 | 4.82 | 5.80 | 5.44 | 5.00 |
| | 37.5 | 5.54 | 4.79 | 4.47 | 5.86 | 5.51 | 5.24 | 6.03 | 5.74 | 5.48 |
| | 50 | 5.61 | 4.84 | 4.54 | 5.97 | 5.65 | 5.38 | 6.15 | 5.92 | 5.64 |

Table 2 continued

| | Disp. dist. (k) | Low pop. (625) | | | Med. pop. (2,500) | | | High pop. (10,000) | | |
|----|-----------------|----------------|------|------|-------------------|------|------|--------------------|------|------|
| | | Null | LHF | HHF | Null | LHF | HHF | Null | LHF | HHF |
| SA | 12.5 | 0.13 | 0.13 | 0.12 | 0.14 | 0.14 | 0.13 | 0.15 | 0.14 | 0.14 |
| | 25 | 0.15 | 0.14 | 0.13 | 0.27 | 0.26 | 0.26 | 0.30 | 0.29 | 0.28 |
| | 37.5 | 0.15 | 0.15 | 0.14 | 0.30 | 0.29 | 0.29 | 0.34 | 0.34 | 0.33 |
| | 50 | 0.23 | 0.22 | 0.20 | 0.33 | 0.32 | 0.31 | 0.52 | 0.51 | 0.50 |

The table includes the three different modeling simulations the null or “pristine” landscape, the low human footprint (*LHF* low road and human development resistances), and the high human footprint (*HHF* high road and human development resistances). Dispersal distances are separated based on biome type (*GS* grassland/shrub, *MC* mixed conifer, *DE* desert, *SA* subalpine)

expected because both GS and MC had the largest starting patch sizes that were likely heavily weighted in the CL metric. In contrast, DE showed smooth (close to linear) changes in LPI in response to changes in life history traits that did not indicate any strong threshold effects. The pattern of change in LPI mirrored that of PLAND in DE. The LPI ranged from 5.3 to 6.2 % for DE, a maximum of a 14.5 % decrease. Among all biomes, SA experienced the most extreme change in LPI (from 0.5 to 0.1 %, an 80 % decrease, and had strong threshold effects where LPI dropped as much as 45–50 %).

Grassland/shrub (GS)

The extent of the GS biome covered over half the Western United States (PLAND was between 53 and 65 %) with 40–60 % of this being a contiguous patch (LPI) across all life-history trait combinations in the “pristine” scenario. Thus, it was no surprise GS was also the most connected of all biome types in the “pristine” scenario (the largest CL among all biome types, Table 2). Habitat loss was also the largest of any biome type for both human footprint scenarios and varied between a 6–14 % loss for LHF and 14–20 % loss for HHF, a percentage difference of 12–27 and 22–37 % relative to the “pristine” scenario. When dispersal ability or population size was low, the losses in LPI were exacerbated (between 35 and 50 %); reaching a low in the HHF scenario of 19.2 %. There were dramatic effects of human footprint on the NP that decreased by over 70 % in most cases. It was only for small population sizes that this trend did not hold and there were large gains in NP (coupled with large decreases in PLAND, LPI and CL) as habitat fragmentation increased in medium and large sized patches.

Mixed conifer (MC)

In the “pristine” scenario, the percentage of the landscape in connected habitat (PLAND) ranged from 17.3–24 % (Table 2), a difference of 28 %. The amount of habitat loss due to the human footprint was slightly higher (a maximum difference of ~32 % in PLAND) than the difference in extent due to life history traits (~28 % difference in PLAND). The greatest habitat loss due to human footprint occurred when population size or dispersal ability were low (e.g., >25 % reduction; Table 1). In contrast, habitat fragmentation occurred at all levels and with the strongest influence at moderate to high population sizes (2,500–10,000) and high dispersal abilities (37.5–50 km). In this zone, LPI and CL tended to decrease rapidly (44–46 % in LPI and 30–34 % in CL) in the HHF scenario, while PLAND decreased less (13–17 %) and coincided with moderate losses to small gains in NP (–10 to 22 %).

Desert (DE)

The DE biome was best characterized as composed of several medium sized patches (initial LPI = 6.15 %) covering 10.4–13.4 % of the landscape in the “pristine” scenario. Habitat loss due to the LHF and HHF scenarios (~21 and ~27 %, respectively) was similar to the difference to the “pristine” scenario (~22 %). Habitat fragmentation caused by human footprint was consistently observed across all life history traits with increases in NP and little change in CL. Habitat loss was most noticeable when populations were small and/or dispersal abilities limited with the largest proportional decreases in PLAND, CL, and in LPI.

Sub-alpine (SA)

For the SA biome type, PLAND was much smaller compared to the other three biome types and ranged between 1.3 and 3.4 % for the “pristine” scenario (a difference of ~62 % due to changes in dispersal ability and population size). The relative impact of human footprint was also much less with decreases in PLAND between 0–0.1 and 0.1–0.3 %, for the LHF and HHF scenarios (a maximum difference of 8 and 17 %, respectively). Most metrics were nearly linear in change (or remained constant) in response to human footprint, and more relative variance occurred in habitat connectivity in the “pristine” scenario. Species with the lowest population size were most sensitive to habitat loss in the human footprint scenarios. Habitat fragmentation due to human footprint was nearly negligible.

Discussion

Research Question 1: Does lower dispersal ability more than smaller population size increase species sensitivity to habitat loss and fragmentation?

Overall, our results indicated that habitat connectivity decreased rapidly and non-linearly, with the decline of either population size or dispersal ability. Metrics that related to the level of interconnected habitat (e.g., patchiness), especially CL, LPI and NP reacted more strongly to changes in dispersal ability than population size. This suggests species with lower dispersal ability, more so than species with low population size, might experience compounded effects with increased habitat fragmentation as their natural dispersal ability already is limiting habitat interconnectedness. Overall, species in the SA biomes are potentially most sensitive over the entire range of dispersal abilities and population sizes due consistent drops observed in CL and LPI over the entire range.

We also found potential critical threshold effects; abrupt, nonlinear changes occurring in an organism’s response across small ranges of habitat loss or fragmentation (With and King 1999). Here, and in Cushman et al. (2010) when either dispersal or population size passed below this threshold, even large increases in the other life-history trait caused very little additional gain in the amount of habitat connectivity. As habitat fragmentation and habitat loss have the potential to impeded dispersal ability (e.g., increased landscape resistance; Fahrig et al. 1995; Dyer et al. 2002) or reduce population (or effective population) size through reduced carrying capacity or genetic diversity (Brook et al. 2008; Dixo et al. 2009) these thresholds are of potential concern. Additional habitat loss or fragmentation may exacerbate sharp declines in population connectivity at these thresholds. Therefore, species with either dispersal ability or population size near and above these thresholds (e.g., in the GS and MC biome) are likely sensitive to future habitat fragmentation and loss.

Research Question 2: What biome type(s) is/are most impacted by the human footprint (roads and land-use)?

Simulation work has suggested major population declines will most often occur when habitat area drops to the range of 10–30 % from the original amount of starting habitat (Fahrig 2001; Flather and Bevers 2002). This was hard to measure precisely, of course, as we studied hypothetical scenarios that estimated potential landscape resistance that were

not empirically derived. In our simulations we did not observe habitat loss to approach the 10–30 % mark, though this result was likely very dependent on the choice of scale. For example, around areas of high relative human impact, it is more likely this level of habitat loss may be present. The largest decrease in habitat extent was observed for species associated with the GS biome (PLAND decreased by 20 %). Much of this was explained by the starting values of PLAND and LPI being highest for the GS biome, and therefore, GS had the highest starting habitat connectivity, making it most sensitive to the human footprint scenarios from the start.

If there is preference in preserving large contiguous patches versus several smaller patches in the GS and MC, the potential change in larger patch sizes (decreased LPI) due to human related events is of greatest interest. The largest contiguous patch in these biomes showed up to a ~50 % shrinkage under the HHF scenario. In response, the CL metric experienced large drops of up to 25 % in the GS biome type and 36 % in the MC biome. The CL metric has been shown to be a strong predictor of the negative effects of habitat fragmentation on population connectivity (Keitt et al. 1997; Cushman et al. 2010, 2013).

We expected that human footprint would have a larger impact on DE associated species than the MC biome. The major reason for this was the high overlap of human development with the DE biome, especially in areas of Southern California and Arizona. Major crop related cultivation takes place in these areas, while there is less human habitation in the MC biome, which is also often more protected (e.g., National forest land and parks). However, our results did not reflect a greater change in the DE biome in fragmentation and loss than in the MC biome. Specifically, the relative change in three of four landscape metrics (PLAND, LPI, CL) from the “pristine” to the human footprint scenarios was greater for the MC associated species than for the DE associated species. One of the major differences between the biome types was the marked loss (e.g., a critical threshold) in contiguous habitat for MC even for high population and dispersal sizes. Because MC showed a highly fragmented distribution to begin with, the MC biome type might also be more sensitive to fragmentation than the DE biome. Though the DE biome was less impacted by habitat fragmentation, the amount of habitat loss was similar in both the DE and MC biome.

Species associated with SA habitats were shown to experience far less relative impact of roads and human land-uses on the extent and fragmentation of habitat. This is not surprising as the SA occupies much smaller average patch sizes that are more isolated, and mostly federally managed with a large portion protected by National Park, National Forest and Wilderness designation.

Research Question 3: Does the human footprint scenarios have a larger impact on habitat fragmentation or loss?

Habitat loss always occurred in response to human footprint (PLAND always decreased, and many times LPI also). The relationship between human footprint, biome type and habitat fragmentation, however, was not as simple. There were cases where rates of fragmentation were higher than habitat loss due to human footprint, but it was heavily dependent on biome type. The SA biome type showed the lowest relative change due to habitat fragmentation or habitat loss out of all biome types, most likely due to the reasons mentioned above (much smaller starting area and the SA biome is largely protected land). We observed for the DE biome type nearly equivalent effects of habitat loss and fragmentation over all species life history traits. The largest effects of habitat fragmentation were observed in the MC and GS biome types.

Habitat fragmentation has been predicted to increase below some threshold habitat composition where habitat area makes up 20–30 % of the total landscape, above which the effects of habitat loss are also greater (Flather and Bevers 2002; Fahrig 2003; Cushman and McGarigal 2004). We observed this strong threshold effect in the MC biome type that, in the “pristine” scenario, represented around 20 % of the total starting habitat area (the entire Western United States). This could potentially explain why even for high dispersal ability and large population size there were steep drops in habitat connectivity relative to total habitat extent (high relative loss in LPI to PLAND, with large decreases in CL). This trend of increased sensitivity to habitat fragmentation at lower levels of habitat connectivity (low population sizes and dispersal abilities) was also observed for the GS biome type. The GS biome was well above the 20–30 % threshold of total starting landscape, species sensitivity to habitat fragmentation noticeable accelerated as habitat extent decreased from the “pristine” scenarios.

Overall, the MC biome experienced increased more sensitivity to habitat fragmentation than habitat loss (the largest relative and most consistent drops in CL). Additionally, there were sharp declines in the area of largest contiguous habitat (LPI) coinciding with only moderate decreases in the total amount of habitat (PLAND) and moderate decreases to small increases in NP. Alone, however, NP is not a pure indicator of habitat fragmentation, as fragmentation is likely increased in this range despite little gain in NP. The reason for this is that medium and large patches were likely fractured into smaller patch sizes. Further, this distinction is potentially more important if one considers large connected patches important for preserving broad-scale population connectivity and biodiversity.

Scope and limitations

Our analysis made assumptions that are worth considering when interpreting results or when drawing any potential implications for conservation purposes. To increase spatial scale to broad applicability while staying within the limitations of using computationally intensive simulations, we were limited in the dispersal ability ranges we could consider (due to large spacing between point seeding); and that were much higher than reasonable for many species under conservation concern. This implies that many taxa with limited dispersal ability, such as invertebrates, reptiles, amphibians and small mammals are not well-represented by these results. However, at this scale, widespread empirical data covering several species is non-existent. Often though, large mammals, and often species with high dispersal ability, are chosen as “umbrella species” for several other taxa (Roberge and Angelstam 2004). Finally, the human footprint scenarios do not well represent flying taxa as they tend to be very mobile and are relatively insensitive to terrestrial resistance features such as roads and human development. All model results, therefore, should be considered most useful for terrestrial (ground-dispersing) animals with dispersal abilities between 12.5 and 50 km.

Conclusion

Our results suggested that the sensitivity of the focal species to the extent of connected habitat was equally dependent on dispersal ability and population size. In contrast, habitat fragmentation is of more concern for species with lower dispersal ability than population size due to the increased sensitivity relative to this life-history trait. We also often observed potential critical threshold effects for both life-history traits where habitat connectivity

quickly declined. Species just above these thresholds could be potentially much more sensitive to future habitat fragmentation and loss. Overall, the human footprint had large effects on the population connectivity of species in the GS and MC biomes, as would be expected given the larger relative starting sizes of these biome types. Habitat loss is generally assumed to have a larger impact on population connectivity than habitat fragmentation except below the threshold where habitat area makes up 20–30 % of the total landscape (Flather and Bevers 2002; Fahrig 2003; Cushman and McGarigal 2004). We observed this increased sensitivity, especially in the MC and GS biome types where there were large decreases in habitat connectivity even at high dispersal ability and large population sizes. Likewise, MC and GS associated species also appeared most sensitive to habitat loss; especially at the largest contiguous patch sizes that are most important for metapopulation viability and biodiversity conservation.

Our work highlights the usefulness of using resistant kernel connectivity modeling to explore habitat and population connectivity for biome associated species across the entire Western United States. Such an approach is generalizable to several species when empirical data is lacking. In addition, it can extend understanding of the complex interaction between life-history traits and landscape resistance, and help to explore the response of habitat connectivity to habitat loss and fragmentation. Our results are available for download, as well as illustrated in a web-based, interactive mapping prototype (<http://ptolemy.dbs.umd.edu/westwide/>) that should be useful for evaluating general habitat connectivity scenarios for the Western United States.

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